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## PHYLOGENY AND ADAPTATION IN THE *ENCELIA* ALLIANCE (ASTERACEAE: HELIANTHEAE)

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### ABSTRACT

The three related genera *Encelia*, *Enceliopsis*, and *Geraea* comprise the alliance. The first consists primarily of shrubs and the latter two of herbaceous perennials and an annual. With the exception of two *Encelia* species of arid South America, all inhabit southwestern North America. *Enceliopsis* and *Geraea* are sister groups, and together form the sister group to *Encelia*, which includes two major clades. Especially in *Encelia*, there are diverse morphologies and a variety of ecological strategies marked by differences in habitat, vestiture, water balance, and photosynthetic parameters. The North American species of all three genera are obligate outcrossers, all with  $n = 18$  chromosomes. Although intergeneric hybrids are largely sterile, interspecific hybrids in *Encelia* are fertile in the wild and in cultivation. Hybrids in the wild are largely restricted to  $F_1$ s, except in areas of human disturbance. Two true-breeding species are of homoploid hybrid origin, and are evidently isolated from the parent species through external ecological barriers involving selection against backcross progeny. Studies of the chloroplast genome and the intergenic transcribed spacer (ITS) of nrDNA show clear differentiation of the genera, but much less variation within *Encelia*, even between phenotypically disparate species, suggesting recent divergence. Because the species are interfertile, it will be possible to study the genetics of the traits that distinguish the species and contribute to their differences.

Key words: Asteraceae, *Encelia*, *Enceliopsis*, *Geraea*, phylogeny

### INTRODUCTION

Section 9.3 of Ehleringer and Clark (1987) is titled “*Encelia*: A model system for the study of adaptation.” Fortunately, perhaps, there are no criteria for “model systems.” In many cases, a model system is simply one that has been well studied, but most model systems also have features that lend them to certain types of research. The lab mouse, *Mus musculus*, is arguably a case of the former, its primary advantage being that it is amenable to captivity. *Drosophila*, *Caenorhabditis elegans*, and *Arabidopsis thaliana* are perhaps in the latter category; each has aspects of its biology that strongly favor certain types of studies. In the study of evolutionary biology of plants, *Clarkia* certainly stands out.

*Encelia* and its relatives certainly aren’t the “new *Drosophila*” or “new *Clarkia*,” but there are features of the group that support studies of the phylogeny of ecological adaptation (as explored by Ehleringer and Clark 1987), the nature of hybrid speciation, the role of breeding barriers in speciation, and the inheritance

of species-diagnostic characters. The purpose of this paper is to outline the state of current knowledge of the genus and point to directions for future research.

The “*Encelia* alliance,” as described here, consists of the genera *Encelia*, *Enceliopsis*, and *Geraea*. They are mostly perennials, all with  $n = 18$  chromosomes, and all inhabitants of arid regions, mainly in southwestern North America.

### PHYLOGENY

Clark (1986) first presented a phylogeny for *Encelia*, and substantially the same tree was published by Ehleringer and Clark (1987). The relationships between *Encelia*, *Enceliopsis*, and *Geraea* were explored by Sanders and Clark (1987), Nishida and Clark (1988), and Nishida (1988). All these studies were based on phenotypic features: capitulum characters, including UV reflectance (Clark and Sanders 1986), trichome type and distribution (Clark et al. 1980; Clark and Clark 1984; Charest-Clark 1984; Charest 1988), and secondary chemistry and associated anatomical features (Budzikiewicz et al. 1984, Proksch and Clark 1984, 1986; Proksch et al. 1988). More recently, Clark

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(1995) provided preliminary phylogenetic data from the internal transcribed spacer of nuclear ribosomal DNA (ITS).

Although these phylogenetic studies have seemed a "work in progress," since full character support for a specific tree has never been published, they agree in a number of major features. First, they strongly support the monophyly of *Encelia* (diagnosed by a constricted apical notch of the achene and the general absence of achene awns; the clade has occurred in every tree in every analysis, with 100% bootstrap and jackknife in combined morphology and ITS [Clark 1995]), *Enceliopsis* sensu stricto (scapose habit and large capitula [Sanders and Clark 1987]; again occurring in all trees), and a sister-group relationship between *Enceliopsis* and *Geraea* (thickened unpigmented crown of the achene [Sanders and Clark 1987]; occurring in all trees). They weakly support the monophyly of *Geraea* and a sister-group relationship between *Enceliopsis* + *Geraea* and *Encelia*.

Within *Encelia*, the presence of two major clades (hereafter called the *frutescens* clade and the *californica* clade) is well supported. *Encelia nutans* Eastwood cannot be clearly assigned to either (ITS data are not yet available), and although phenotypic data clearly assign *E. ravenii* Wiggins to the *frutescens* clade, ITS data less clearly assign it to the *californica* clade. Within the clades, relationships are less certain. For example, a stepwise increase in leaf pubescence and congestion of the paniculate capitulescence seem to show relationships among *E. farinosa* A. Gray, *E. canescens* Lam., *E. palmeri* Vasey & Rose, and *E. halimifolia* Cav. in the *californica* clade, but their ITS sequences show virtually no differences.

*Flourensia* has been traditionally viewed as an outgroup to the *Encelia* alliance (Clark 1986), and ITS data appear to support this. Preliminary sequences suggest that two "misfits" in *Encelia*, *E. stenophylla* E. L. Greene and *E. scaposa* (A. Gray) A. Gray, are more closely related to *Flourensia* than to the *Encelia* alliance. Morphology and biogeography provide some support to this view (Clark unpubl.)

### *Geraea*

This genus consists of two species, *G. viscida* (A. Gray) S. F. Blake, an eradiate herbaceous perennial with sessile glandular leaves, and *Geraea canescens* Torr. & Gray, a radiate annual with alate-petioled pilose leaves (Fig. 1). Even though they have long been congeners, they are superficially dissimilar. In her study of the genus, Nishida (1988) demonstrated additional differences, but suggested that the genus is monophyletic, diagnosed by strongly obtuse achenes (common in the Heliantheae, but otherwise unknown in the *Encelia* alliance) and a tapered disk

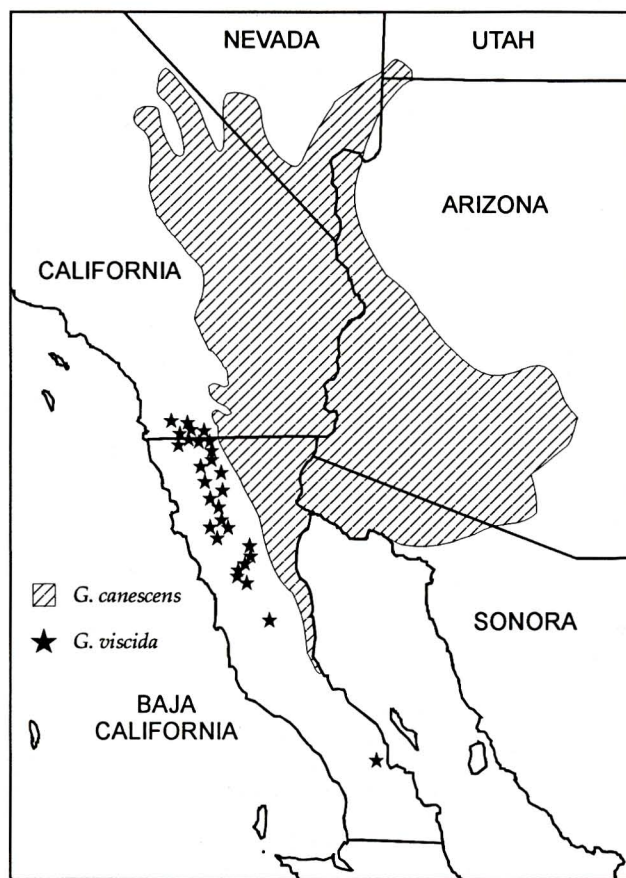


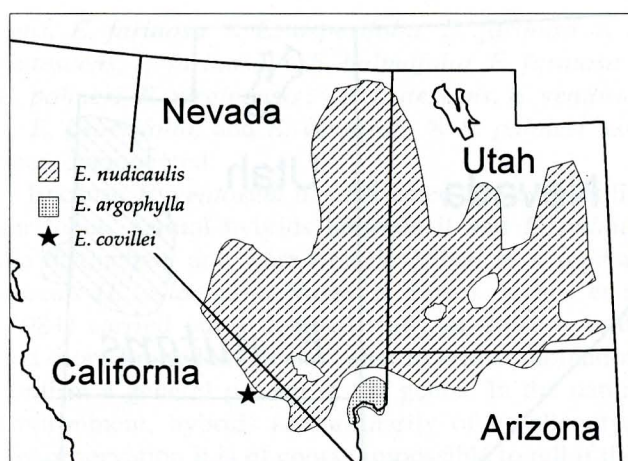
Fig. 1. Distribution of *Geraea*.

corolla throat (as contrasted with the bulbous throat of the relatives). Although Proksch et al. (1986) showed phytochemical similarities between *G. canescens* and *Enceliopsis*, they found a different set of chemical constituents in *G. viscida*. ITS sequences are preliminary, but the clade occurred in 72% of 799 most parsimonious trees in an analysis of ITS1 (Clark unpubl.).

*Geraea canescens* hybridizes in the wild with *E. farinosa* (Kyhos 1967) and *E. frutescens* A. Gray (Clark unpubl.). Although this has suggested close relationship, it is important to realize that these two species are the only members of the alliance with which *G. canescens* is sympatric. In cultivation, *G. canescens* has been successfully crossed with several other *Encelia* species (Clark unpubl.). Two important facts emerge from this study. First, all hybrids between *G. canescens* and other species are sterile (Kyhos 1967, found asynapsis in *G. canescens* × *E. farinosa* hybrids). Second, *G. canescens* is always the pollen parent; no other species will successfully pollinate *G. canescens*. This unilateral incompatibility is not unexpected, since *G. canescens* is an annual (thus highly disadvantaged by loss of eggs to sterile hybrid progeny) and all the other species are perennials.

Of course, the *G. canescens* × *G. viscida* hybrid would be very interesting. Is it sterile? How do the



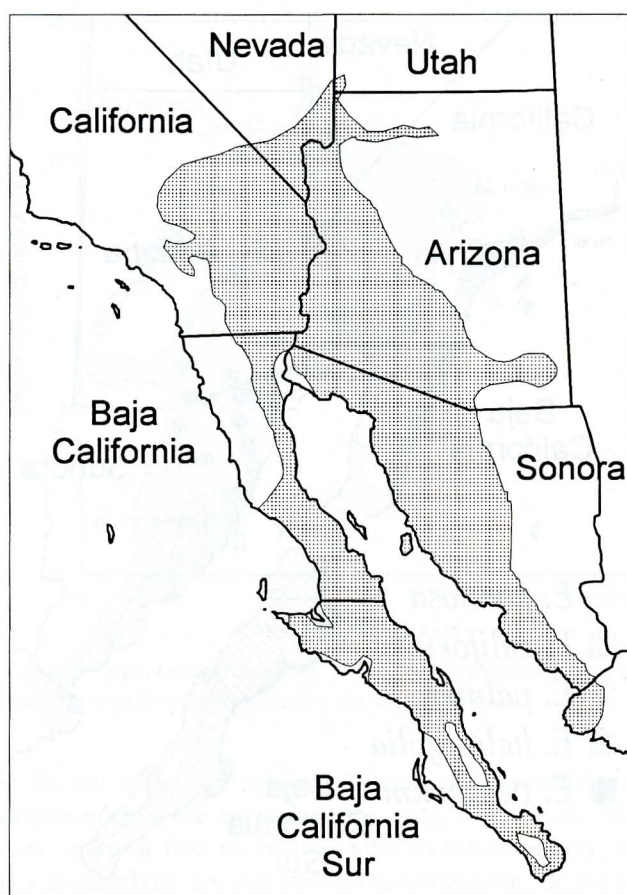
Fig. 2. Distribution of *Enceliopsis*.

contrasting features of the parents sort out? Clark (unpubl.) and Nishida (1988) made numerous attempts to form this hybrid. As expected, all attempts using *G. canescens* as the ovulate parent resulted in no fruit set. When *G. viscida* was the ovulate parent, all the progeny were indistinguishable from *G. viscida*; evidently the *G. canescens* pollen had overwhelmed the self-incompatibility system of *G. viscida*, allowing self-pollination. Attempts to circumvent this by excising *G. viscida* anthers resulted in ovule abortion. Thus, no hybrids were ever formed.

### *Enceliopsis*

*Enceliopsis* consists of three species of suffrutescent, generally scapose perennials with large capitula (*Encelia nutans* spent most of its nomenclatural history in *Enceliopsis*, but it shares the achene synapomorphy with *Encelia* and no synapomorphies with *Enceliopsis*, so it is considered here in *Encelia*, where it was originally described). As mentioned above, the monophyly of the genus is well established. One species, *E. nudicaulis* (A. Gray) A. Nels., is widespread across the Great Basin, whereas the other two are restricted endemics, *E. argophylla* (D.C. Eaton) A. Nels. occurring on gypsum soils around Lake Mead in Nevada, and *E. covillei* (A. Nels.) S. F. Blake being found only in a few canyons on the west slope of the Panamint Mountains west of Death Valley, California (Fig. 2). The latter two are similar in appearance, were once considered conspecific, and share features that can best be interpreted as apomorphies (Sanders and Clark 1987). However, preliminary ITS data seem to ally *E. covillei* and *E. nudicaulis*.

Sanders and Clark (unpubl.) formed hybrids, *E. nudicaulis* × *E. covillei* and *E. nudicaulis* × *E. argophylla*, but neither survived long enough to examine their fertility (all members of the genus are difficult in cultivation). Like *Geraea* and almost all *Encelia*, the species of *Enceliopsis* seem to be self-incompatible.

Fig. 3. Distribution of *Encelia farinosa*.

### *Encelia*

*Encelia* comprises 15 species, the aforementioned *E. nutans* an herbaceous perennial, and the rest shrubs. Two are South American: *E. hispida* Anderss. from some of the Galápagos Islands and *E. canescens* from Perú, Chile, and Argentina. The rest inhabit southwestern North America.

The genus contains two well-marked clades. The *californica* clade (Fig. 3, 4), consisting of *E. californica* Nutt., *E. canescens*, *E. densifolia* Clark & Kyhos, *E. farinosa*, *E. halimifolia*, *E. hispida*, *E. palmeri*, and *E. ventorum* Brandege, is diagnosed by a unique benzopyran-benzofuran dimer (Proksch and Clark 1986) and ultraviolet-reflecting ray corollas (Clark and Sanders 1986). All but *E. densifolia* also share brown disk corollas. The *frutescens* clade (Fig. 5), comprising *E. actoni* Elmer, *E. frutescens*, *E. resinifera* C. Clark, and *E. virginensis* A. Nels., is marked by few or no benzopyrans or benzofurans, a lack of resin ducts (Proksch and Clark 1986), and erect fruiting heads with expanded paleae (Clark 1986). *Encelia ravenii* (Fig. 6) shares these features, but ITS sequences ally it instead with the *californica* clade; both data sets need to be re-examined.

Perhaps because of its unusual habit, *Encelia nutans*



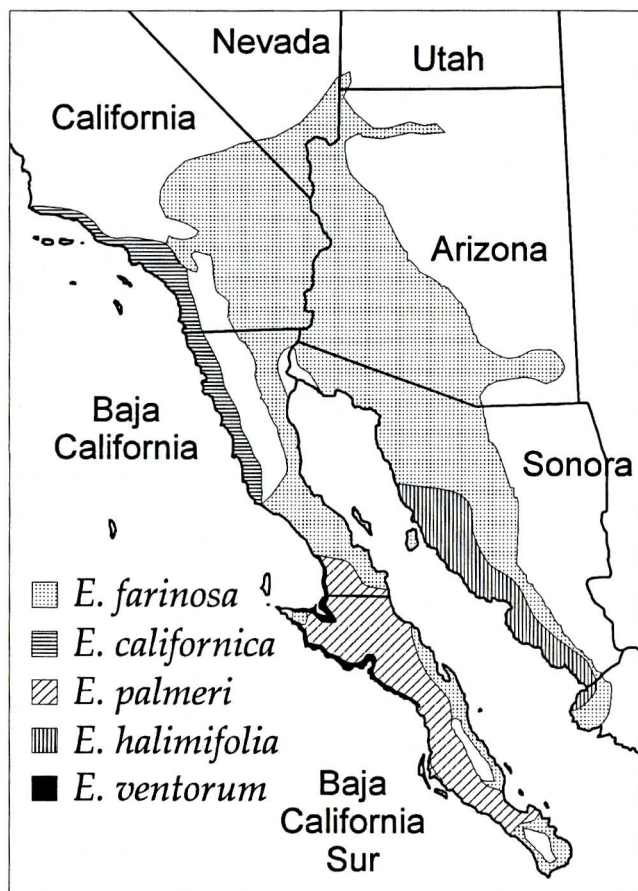


Fig. 4. Distribution of other members of the *californica* clade, overlapping the distribution of *E. farinosa*.

(Fig. 6) has no clear-cut synapomorphies tying it to either clade, and no molecular data are yet available. It perennates as a thick underground semisucculent rootstock, emerging during the winter and spring to flower and fruit, with the above-ground parts withering in the summer. Its biology is in need of detailed study.

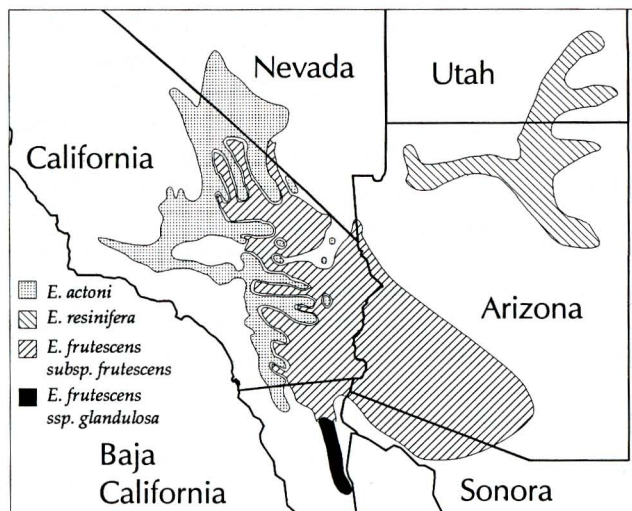


Fig. 5. Distribution of the *frutescens* clade.



Fig. 6. Distributions of *Encelia nutans*, *E. ravenii*, and *E. densifolia*.

Because it is difficult in cultivation, no data pertaining to self-incompatibility or hybridization are available.

With the exception of *E. canescens*, and the probable exception of *E. hispida*, all the species are self-incompatible. Even *E. canescens* does not ordinarily spontaneously self. Pollination is generalist, involving butterflies, solitary bees, occasional honeybees, and beetles (Clark, unpubl. observations).

All the species of *Encelia* are interfertile in cultivation, and their  $F_1$ s are fertile, as well as all studied  $F_2$ s and backcrosses. Spontaneous natural hybrids are common in areas of sympatry. *E. actoni*  $\times$  *E. frutes-*



*cens*, *E. farinosa* × *E. asperifolia*, *E. farinosa* × *E. frutescens*, *E. farinosa* × *E. halimifolia*, *E. farinosa* × *E. palmeri*, *E. virginensis* × *E. frutescens*, *E. ventorum* × *E. asperifolia*, and *E. ventorum* × *E. palmeri* have been documented.

Because *E. ventorum* has dissected leaves with linear lobes, natural hybrids between it and *E. palmeri* are distinctive, and were first described as a separate species (*E. ×laciniata* Vasey & Rose). Kyhos et al. (1981) carried out a detailed study of those hybrids, and more limited studies of other hybrid combinations confirm a general pattern in the genus. In the natural environment, hybrids are ordinarily of F<sub>1</sub> phenotype (by observation it is of course impossible to tell if they are actually F<sub>1</sub>s). To the extent that the parent species show a clear separation of habitat, the hybrids are found in areas of intermediate habitat. In areas of human disturbance, and occasionally in areas of natural disturbance, F<sub>2</sub> and backcross plants may be found, but these are otherwise rare. Progeny tests show, however, that these recombinant forms are produced far in excess of their appearance in the habitat; Kyhos et al. (1981) showed that most seeds produced by *E. ×laciniata* at a certain locality were backcrosses to one parent species or the other (as expected, since the F<sub>1</sub>s were in much lower frequency than the parents), but not a single backcross individual was seen in the population.

All this suggests that, whereas F<sub>1</sub> hybrids may in some cases have adaptive features allowing them to persist, backcrosses and F<sub>2</sub>s (except perhaps those that resemble F<sub>1</sub>s) are at a severe selective disadvantage, in many cases being totally eliminated from the population. The cause of this harsh selection against non-F<sub>1</sub> progeny is unknown, but the effect is clear-cut.

#### SPECIES OF HYBRID ORIGIN

Factors affecting interspecific hybridization in *Encelia* become all the more important, because two species show clear evidence of having originated from hybrids (Clark and Kyhos 1979; Clark et al. 1980; Allan et al. 1993, 1997; Clark and Allan 1997). *Encelia virginensis* A. Nels. appears to have originated from hybrids of *E. actoni* and *E. frutescens* subsp. *frutescens*, and *E. asperifolia* (S. F. Blake) Clark & Kyhos from hybrids of *E. californica* and *E. frutescens* subsp. *glandulosa* C. Clark.

Although Riesberg and Ellstrand (1993) have pointed out the difficulties in inferring hybrid origin, there are nevertheless three somewhat independent lines of evidence that in combination can support such hypotheses. First, species of hybrid origin may be intermediate between their parent species (although in a number of documented cases they are not, and species that appear intermediate have not infrequently proven

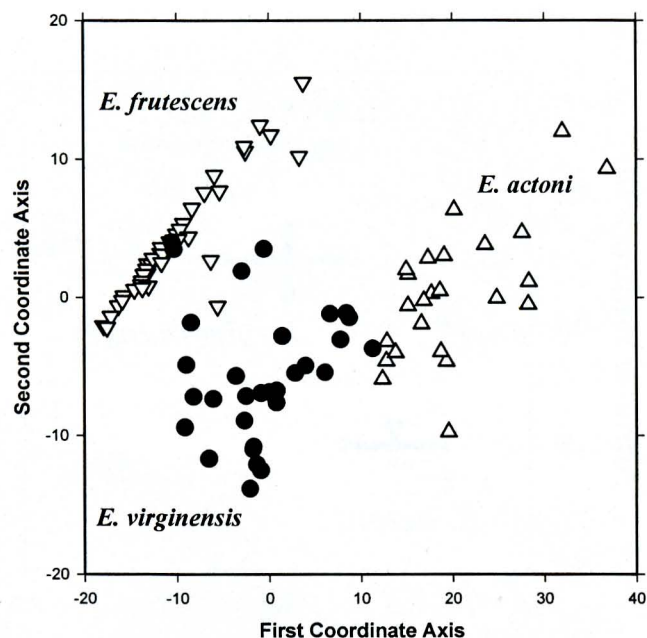


Fig. 7. *Encelia virginensis*, *E. actoni*, and *E. frutescens*, first two principle coordinate axes (see text for explanation).

to be not of hybrid origin). Second, species of hybrid origin may agree in phenotype with F<sub>1</sub> hybrids. This may seem at first to be the same as intermediacy, but F<sub>1</sub>s themselves are not always intermediate, or are intermediate in specific ways. Third, species of hybrid origin may share features of the parent species that otherwise would be autapomorphies of those species, thus producing a pattern of shared characters that could not be easily explained by divergent evolution. Even in combination, these criteria can never prove that a species is of hybrid origin, but they can provide a weight of evidence.

*Encelia virginensis* A. Nels. is generally intermediate between its parents. Measurements were made of pedicel width, number of rays, ray corolla length, leaf length, leaf width, petiole length, capitulum height, and capitulum width of 119 *E. virginensis*, *E. frutescens*, *E. actoni*, and *frutescens* × *actoni* F<sub>1</sub> hybrids. These measurements were analyzed by principal coordinate analysis; both the *E. frutescens* plants and F<sub>1</sub> hybrids appear between the putative parents in a plot of the first two coordinate axes (Fig. 7).

Length and width of ten achenes each from five populations of *E. actoni* and *E. frutescens* and two populations of *E. virginensis* were measured. *Encelia virginensis* was intermediate to the parent species in both length and width; it differed significantly (*t*-test, *P* < .05) from both parents in width, but not in length (Fig. 8). *Encelia virginensis* also inhabits a climate somewhat intermediate to the parents (Fig. 9), but with a slightly greater annual range of temperature, consistent with its more interior distribution (Fig. 10).

Plants of *E. virginensis* are normally indistinguish-



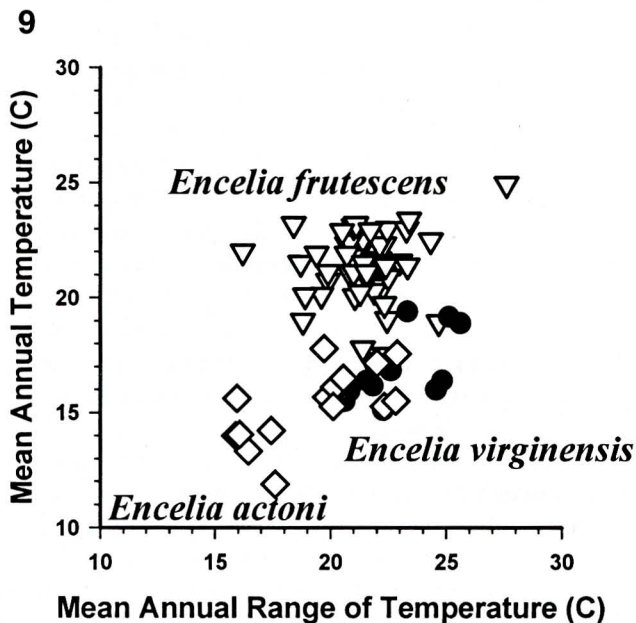
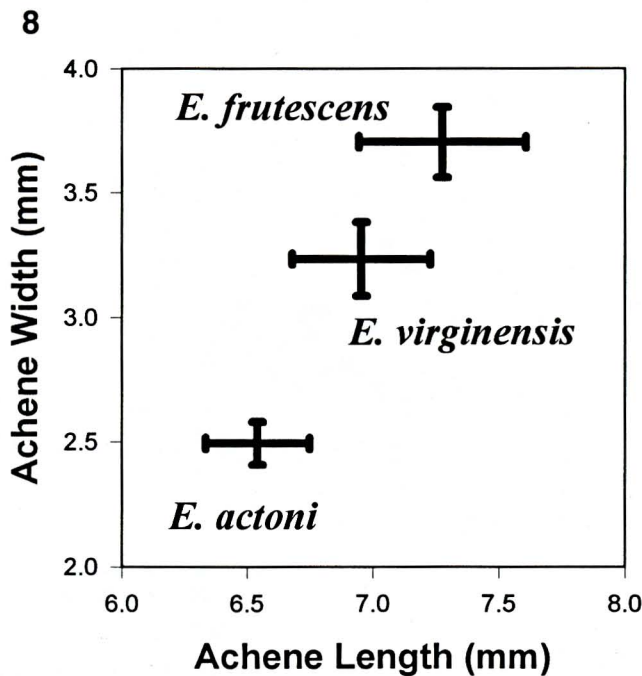


Fig. 8, 9. *Encelia virginensis*, *E. actoni*, and *E. frutescens*—8. Length and width of achenes (error bars represent the 95% confidence level)—9. Climatic distribution.

able from  $F_1$  hybrids between *E. actoni* and *E. frutescens*. (Prior to molecular studies, only the presence of populations of similar and apparently true-breeding *E. virginensis* plants hundreds of kilometers from either parent supported the idea that *E. virginensis* was a species, rather than a named hybrid.) Figure 11 shows the leaf trichomes of all three species and the  $F_1$ .

*Encelia virginensis* shares apomorphies with both parents. With *E. frutescens* it shares broad multicellular-based uniseriate leaf hairs (Clark et al. 1980, Ehleringer and Cook 1986). Since *E. actoni* has no clear

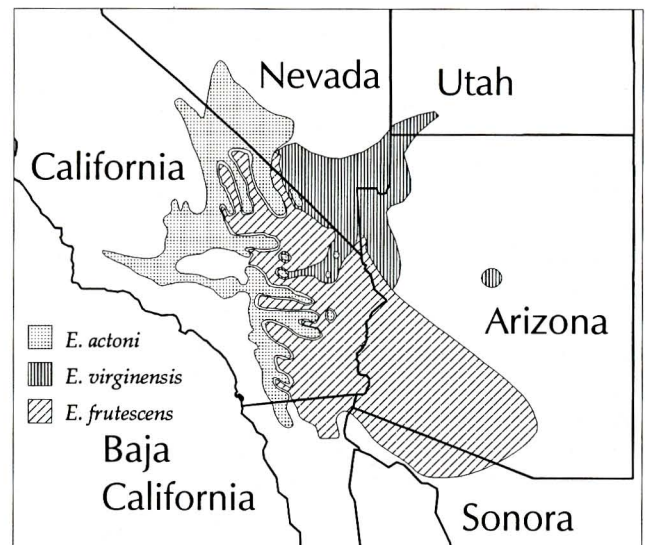


Fig. 10. *Encelia virginensis*, *E. actoni*, and *E. frutescens*, geographic distribution

phenotypic autapomorphies, *E. virginensis* shares none with it. However, it shares several random amplified polymorphic DNA (RAPD) markers with both parents (Allan et al. 1993, 1997).

In addition, the internal transcribed spacers of nuclear rDNA (ITS) of several individual *E. virginensis* combine the sequences of both parents in a manner strongly suggestive of hybrid origin. The parent species differ by 9 bases; at each site, every sampled *E. virginensis* has either the *E. actoni* base, the *E. frutescens* base, or a polymorphism consisting of both bases. Furthermore, few of the individuals are identical to each other, suggesting a "sorting out" of parental lineages (Clark in prep.).

*Encelia asperifolia* is less precisely intermediate to its parents, and in fact was originally described as a subspecies of *E. californica* (Clark and Kyhos 1980). Its achenes are smaller in both length and width than either parent (Fig. 12). It has capitula similar to those of *E. californica*, with long ray florets (as contrasted with the eradiate condition of *E. frutescens*), but leaves more like those of *E. frutescens*, so much so that sterile specimens are occasionally identified as that species, leading to the incorrect distribution of *E. frutescens* in Baja California provided by Wiggins (1980).

Unlike *E. virginensis*, *E. asperifolia* is allopatric to one of its parents (*E. frutescens*) and only parapatric to the other (Fig. 14). It occupies climates, however, that are intermediate between the climates of the parent species (Fig. 13). *Encelia asperifolia* plants are not especially similar to  $F_1$  hybrids, the latter being more or less intermediate to the parents.

With *E. frutescens*, *E. asperifolia* shares broad multicellular-based uniseriate leaf hairs (Clark et al. 1980, Ehleringer and Cook 1986), and an absence of benzopyrans or benzofurans (Proksch and Clark 1986), as



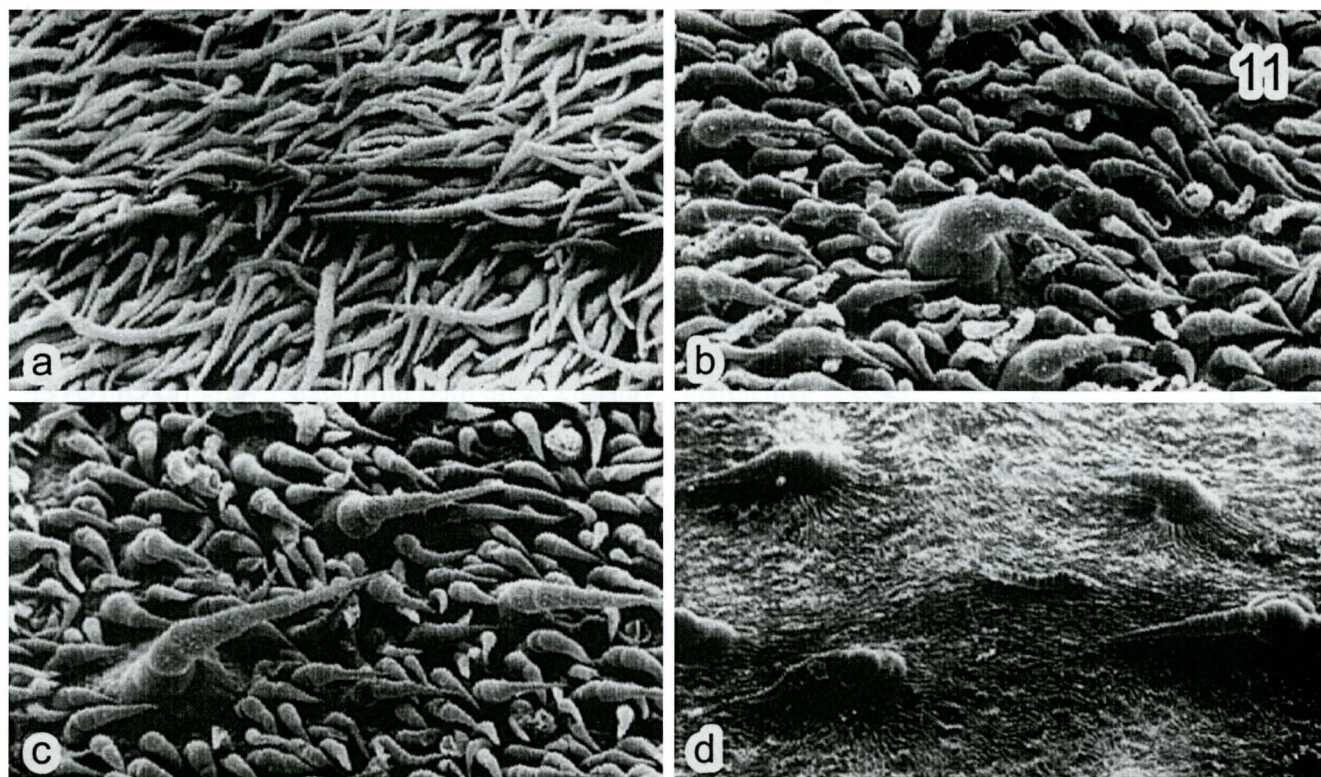


Fig. 11. Leaf trichomes: (a) *Encelia virginensis*, (b) *E. frutescens*, (c) *E. actoni*, and (d) *E. actoni*  $\times$  *frutescens*.

well as two RAPD markers (Clark unpubl.). With *E. californica* it shares UV-reflective ray corollas (Clark and Sanders 1986), brown disk corollas, moniliform hairs (Clark et al. 1980, Ehleringer and Cook 1986), and five RAPD markers (Clark unpubl.).

Like *E. virginensis*, the single sequenced *E. asperifolia* appears to have chimeric ITS. The parent species differ by 21 bases. *Encelia asperifolia* has *E. californica* bases at eight sites, *E. frutescens* at seven, unique bases at four sites (including a site for which the parents are identical), and ambiguous bases at three. Its unique ITS mutations, its lack of precise intermediacy, and its disjunct distribution suggest that *E. asperifolia* is an older species than *E. virginensis*.

#### Theoretical Mechanisms

Riesberg (1991) and Riesberg et al. (1990, 1995) have outlined a mechanism for hybrid speciation in *Helianthus* that agrees with the "recombinational speciation" model proposed by Grant (1981). In these examples from *Helianthus*,  $F_1$ s have reduced fertility. The  $F_2$ s are often more fertile than backcrosses, and repeated crossing among  $F_2$  and later generations restores fertility in the new hybrid species through recombination of chromosome segments (in essence, the entire genome becomes chimeric). Thus, the newly forming species is isolated from the parents by internal reproductive barriers. Other documented cases of hy-

brid speciation (Arnold 1993; Gallez and Gottlieb 1982) involve similar mechanisms.

Hybrid speciation in *Encelia* differs from this model in many respects. In *Encelia*,  $F_1$ s are fully fertile, and there are few or no chromosomal differences between parent species. Backcrosses are formed as readily as  $F_2$ s, but are strongly selected against, and seldom occur as mature plants in the wild. This corresponds to another model proposed by Grant (1981), hybrid speciation with external barriers. Although he included such mechanisms as pollinator fidelity in "external barriers," the strong selection against backcross progeny serves the same purpose.

#### XEROPHYTIC ADAPTATIONS

All species of the three genera *Encelia*, *Enceliopsis*, and *Geraea* inhabit arid regions, and all have adaptations to the seasonal lack of water that characterizes them. These adaptations have been extensively studied by Ehleringer and his colleagues (summarized in Ehleringer and Clark 1987). Four different mechanisms serve different species in the group.

*Geraea canescens* is an annual, and thus a drought-avoider. Although annuals are very common in the regions inhabited by members of the *Encelia* alliance, they are uncommon among the group of Heliantheae to which it belongs.

*Encelia farinosa* exemplifies leaf shading by thick



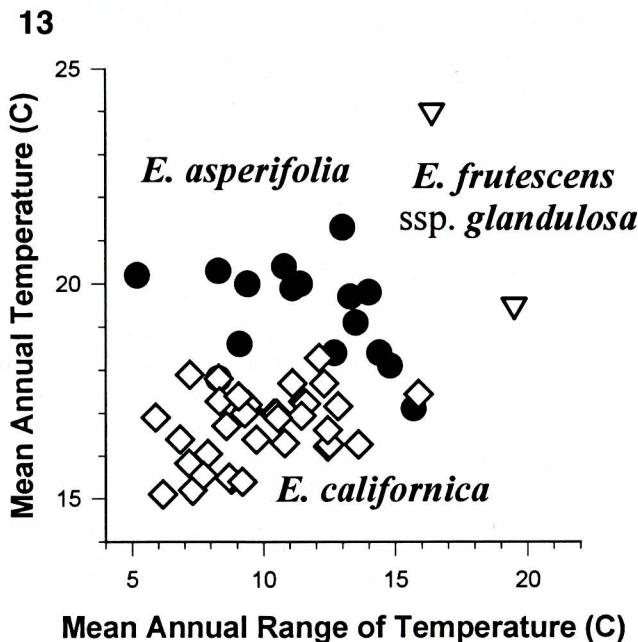
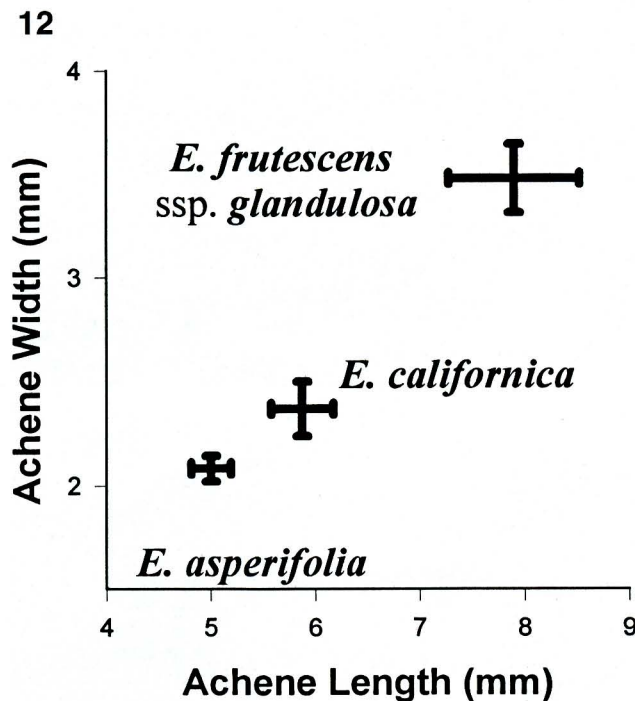


Fig. 12, 13. *Encelia asperifolia*, *E. californica*, and *E. frutescens* subsp. *glandulosa*—12. Length and width of achenes (error bars represent the 95% confidence level)—13. Climatic distribution.

reflective pubescence. This shading reduces leaf temperatures, preventing leaf damage even when there is inadequate water for transpirational cooling. *Encelia palmeri*, *E. canescens*, *E. actoni*, *E. ravenii*, and the three species of *Enceliopsis* all have reflective pubescent leaves, and although they have not been studied as extensively as *E. farinosa*, the same mechanism can be inferred. *Encelia densifolia* is especially interesting in that its pubescence is wettable, and is much more

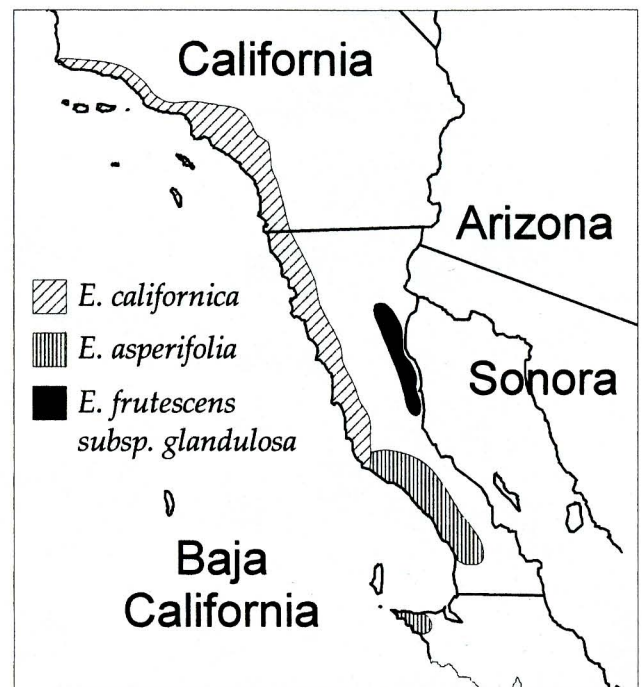


Fig. 14. *Encelia asperifolia*, *E. californica*, and *E. frutescens* subsp. *glandulosa*, geographic distribution.

reflective when dry than when wet with fog (Harrington and Clark 1989).

Within the alliance, reflective pubescent leaves would seem to be ancestral, but the outgroup *Flourensia* has generally glabrous glutinous leaves, a condition not found in the *Encelia* alliance. An understanding of the relationships of these two groups among the rest of the Heliantheae will clarify the ancestral condition in the *Encelia* alliance.

*Encelia californica* is an example of a drought-deciduous species; it loses its glabrous leaves in the dry season. It inhabits coastal climates that are wetter than the typical desert haunts of the other species, but its range is characterized by no precipitation during the six warm months. *Geraea viscida* and *Encelia nutans* are also drought-deciduous, in both cases losing the above-ground parts of the plant. *Encelia halimifolia* is nearly as glabrous as *E. californica*, but the nature of its adaptation is not well understood.

*Encelia frutescens* exhibits the other adaptation used by glabrous-leaved species: transpirational cooling. It lives primarily in desert washes and other areas with water at depth, and thus can continue to transpire into the dry season. (It, too, loses its leaves when the water runs out, but that does not always happen.) *Encelia ventorum* lives on coastal sand dunes, another habitat with deep water, and most likely uses the same mechanism.

#### ECOTYPES OF *ENCELIA FARINOSA*

*Encelia farinosa* is the most widespread species in the genus (Fig. 3). It contains three infraspecific taxa,



two (f. *farinosa* and f. *phenicodonta* S. F. Blake) differing only by disk color (Kyhos 1971), and the third (var. *radicans* Brandege) lacking the characteristic leaf pubescence.

Other variation is not taxonomically distinguished. The plants of cismontane southern California (in western San Bernardino and Riverside counties) differ in vegetative appearance from those of the adjacent Colorado Desert, being taller and less "dome-shaped." These "ecotypes" meet and to some extent intergrade in the San Gorgonio Pass.

Miller (1988) grew plants from both areas in common gardens in both areas. He found that the leaves of desert-origin plants were significantly more reflective (around 50% reflectance) at 670 nm (the red absorption peak of the photosynthetic action spectrum) than cismontane-origin plants (30–40%) in both test gardens. Cismontane-origin plants had significantly longer peduncles (20–22 cm) than desert-origin plants (10–15 cm) in both test gardens. These results imply a genetic difference between the two "ecotypes" for these traits. However, even though cismontane plants growing in habitat had a significantly greater height/width ratio than desert plants (a measure of the "dome"-shape of the latter), this difference did not persist in the test gardens, suggesting phenotypic plasticity.

The maintenance of these differences across a narrow geographic region suggests substantial selection pressures, and indeed the contact between the two forms in San Gorgonio Pass also marks a transition from a generally coastal flora to a desert flora. This region most likely represents a secondary contact between the forms. The cismontane form is otherwise isolated from the bulk of the species.

#### EVOLUTION OF *ENCELIA*

Although the species show some striking differences in morphology and ecology, the low levels of variation in ITS and the chloroplast genome and the ability of all the species to interbreed suggest a recent origin, especially as compared to the sister group comprising *Enceliopsis* and *Geraea*. Despite the recent origin, and despite the potential for hybridization, the species are easily distinguished. Most taxonomic confusion has resulted from the overrepresentation of hybrids in herbarium collections (the, "I don't recognize that plant so I'll put one in the press," syndrome).

More important, the basic pattern of evolution in the group appears to be divergent. Grant (1981) characterized similar situations in other genera as "syngamea"; by this reckoning, the genus *Encelia* would be a syngameon, equivalent to a single "biological" species, and the individual taxonomic species would be "semispecies." However, both morphological and mo-

lecular evidence clearly support a branching cladogram. There is no evidence of introgression in the genus, and excepting the two species of hybrid origin, no evidence of reticulation. Clearly the mechanisms that restrict backcrosses in the natural environment thus restrict gene flow between the species.

This divergent evolution has led to clear morphological and ecological differentiation among the species. Because the species are so easily grown and hybridized in cultivation, *Encelia* provides a great opportunity to directly study the inheritance of traits that distinguish species.

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